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VI.

CONTRIBUTIONS FROM THE CRYPTOGAMIC LABORATORY OF THE MUSEUM OF HARVARD UNIVERSITY.

VII. — ON THE STRUCTURE OF THE FROND IN CHAMPIA PARVULA, Harv.

By Robert Payne Bigelow.

Presented June 16, 1887.

There is a small group of the *Florideæ*, consisting of the genera *Chylocladia*, *Lomentaria*, and *Champia*, that is of particular interest from the entirely anomalous condition of the frond. The frond is hollow, is generally chambered, has thin walls, and contains peculiar filaments running longitudinally close to the inner wall. Of this group, *Champia parvula* and *Lomentaria Baileyana* are abundant along the New England coast south of Cape Cod. The former species being the more convenient, was selected from a study which I began in November last at the suggestion of my instructor Dr. W. G. Farlow.

In order to understand the points at issue, it is first necessary for us to get a general idea of the structure of the plant that we are studying. In general aspect the frond of *Champia parvula* is jointed, cylindrical, and much branched; forming a tuft four to six centimeters high. The branches are given off at the joints, or constrictions; either singly, or else in pairs, or whorled (Plate, Fig. 1). If a portion of the frond be cut open lengthwise and examined with a low power of the microscope, it will be seen to be chambered, the barrel-shaped chambers being separated by cellular diaphragms and becoming progressively smaller towards the apex (Figs. 1, 2). The diaphragms are always at the joints or constrictions above referred to.

A little more careful attention will reveal a number of straight filaments (Fig. 2, *f*) running from the base of a branch to its tip, where they converge. As far as my observations go, the number of filaments in a branch may vary from eleven to fifteen. It will be noticed that all the filaments in each chamber have projecting from their inner side one or two little globular or pear-shaped cells (Diagram, B). *Bulb-cells* we might call these for want of a better name. With a little higher power than is necessary for making out these

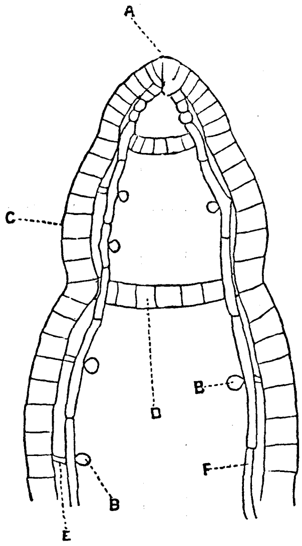

DIAGRAM OF A LONGITUDINAL SECTION OF A TIP OF C. PARVULA.

A, the apex; B, bulb-cell; C, cortex; D, diaphragm; E, connection between filament and cortex; F, filament.

points, one may observe that each filament is composed of a single row of long cylindrical cells united by their ends. There are three or four of these cells to a chamber. The bulb-cell is always in the neighborhood of the middle of the filament cell to which it is attached; and opposite to it, that is, on the outer side, the filament is usually connected with the cortex, often by means of a short slender cell. The filaments pass through the diaphragms practically unchanged. Usually it is the middle part of the penetrating filament cell that is in immediate contact with the diaphragm, and the ends of two filament cells never meet in the plane of the diaphragm. Moreover, this filament cell that penetrates the diaphragm never bears a bulb-cell, as far as I have seen. I can discover no direct connection between the filaments of one branch and those in the rest of the plant. They merely converge into a small space at the base of the branch opposite the diaphragm of the main stem, and there they end.

The wall of the frond, or cortex, and the diaphragms, are each composed of a single layer of cells very similar in size and shape. In shape these cells are somewhat flattened on their free sides, while those portions in contact are polygonal. Of the three dimensions of the cell, the one at right angles to the layer is the shortest in the adult cells of both the diaphragms and the cortex. In the older cells of the cortex the longitudinal diameter tends to become the longest. Towards the tip of the plant, the radial diameter of the cells of the cortical layer does not decrease much until very near the apex, but the other two diameters decrease more rapidly, so that the cells become columnar (Fig. 2). The whole plant is covered with an apparently gelatinous cuticle, and the chambers contain what appears from alcoholic material to be a viscid fluid. It becomes hardened in alcohol, and is easily stained.

All this is by way of introduction to a more careful examination of the tip of the plant, which it will be necessary to make in order to see just how growth takes place there, and to discover, if we can, how the cells of the cortex and of the longitudinal filaments arise, and what is the origin of the bulb-cells and of the diaphragms. The material that I used in my attempt to answer these questions was collected by Dr. Farlow at Wood's Holl, and preserved in moderately strong alcohol. From the smallness and delicacy of the object to be studied, and the consequent difficulty of making free-hand sections, it was evident that nothing more was to be discovered by that means than what I have already described. I therefore attempted to apply the methods now in use by all animal histologists, of imbedding in paraffine and sectioning with the microtome into ribbons. As the tissues of this plant contain larger cavities with comparatively very thin walls my chief difficulty was to get this tissue into the paraffine without allowing it to collapse. Another difficulty was that when I stained with aniline colors they would become washed out during the subsequent manipulation.

Both difficulties were avoided quite successfully in the following manner. My material was put into 70% alcohol. From this, portions that I wished to section were transferred to 90% alcohol to harden. After being hardened, the specimen was stained. If it was to be stained with some coal-tar color, I used a very strong solution in 90% alcohol. If I wanted to get a hæmatoxylin stain, I transferred the specimen back to 70% alcohol and used Klemenberg's method, or, more frequently, this method with the calcium chloride omitted. After remaining in the stain about forty-eight hours, if the stain was hæmatoxylin, the specimen was partly decolorized in the usual manner with very dilute hydrochloric acid in 70% alcohol; if the stain was some aniline, the surplus stain was simply washed out in the 90% alcohol into which the specimen was always put next. From 90% alcohol it was transferred to absolute alcohol, then allowed to sink through alsolute alcohol into chloroform, then put into pure chloroform. I then used a slight modification of the familiar chloroform method of imbedding in paraffine. I employed three mixtures of soft paraffine and chloroform. No. 1 was a saturated solution; No. 2 was two volumes of No. 1 plus one volume of chloroform; No. 3 was one volume of No. 1 plus two volumes of chloroform. The preparation was passed from pure chloroform into No. 3, into No. 2, and then into No. 1. After the preparation was thoroughly saturated with solution No. 1, the vial was uncorked and warmed until the chloroform was all evaporated, or very nearly so. After this the specimen was put into the soft paraffine bath, from this into the hard paraffine, and then imbedded, sectioned in ribbons, and mounted with Schällibaum's fixative and benzole balsam in the usual way.

In staining I obtained the best results with hæmatoxylin. It brings out the cell walls and nuclei well. Eosin shows the protoplasmic contents of the cells better, but leaves the boundaries indistinct. I obtained fair results with methyl-violet and safranin.

It may be well before proceeding farther to examine the literature that has already appeared bearing on our subject. The first publication of interest in this connection is by Carl Nägeli. In "Die Neuern Algensystem," (Zurich, F. Schulthess, 1847, p. 246,) he treats of the structure of *Lomentaria kaliformis* and of its method of growth. After describing the thallus as hollow, jointed, and with whorled branches, the joints being separated by cellular diaphragms, he goes on to say that at the tip of the branch there is an apical cell (Scheitelzelle) which he supposes to divide by oblique partitions. He does not seem to have made this out very clearly, however. He says that the wall of the thallus is two-layered, and he points out that in the younger portion each of the outer cells abuts against a smaller inner cell. The outer cells divide perpendicularly to the thallus, each into three or more, and thus the cortex is formed; while the inner cells do not divide, but become extended longitudinally and form the longitudinal filaments. Nägeli finds fifteen of these filaments in the adult frond. Their component cells are so elongated that it only takes two of them to reach the length of a joint. Upon the inner side of each of these cells near its middle there is a small globular or pear-shaped cell, or sometimes two or three of them whorled. He says they seemed to be formed by an outgrowth from the long cell.

A paper appeared in 1882 * by Dr. G. Berthold, in which he incidentally gives a general description of structure and method of growth in *Champia parvula, Lomentaria kaliformis, Chylochladia reflexa,* Harv., and *Ch. mediterranea,* J. Ag.

He gives a diagram of the tip of *Champia parvula,* and points out that there is not a single apical cell, but a group of them, and according to him they are arranged in a very definite way. At the apex four of these cells form a cross, only two of them however meeting in the middle. From the outer side of each of these cells is given off a row of cells derived from this apical cell, and very gradually increasing in width. In the angles of the cross thus formed are four other apical cells which give rise to similar rows; and then the remaining space is filled by a third series, usually of eight apical cells and their progeny, making in all sixteen rows of cells each headed by an apical cell. The cells of these rows are flattened at right angles to the axis, and give rise to other cells by oblique division. According to Berthold, these second cells may divide again in like manner, thus forming the peripheral covering cells, while the first do not divide, but become much enlarged.

Berthold was the first to point out that the longitudinal filaments of the adult frond correspond exactly in number and position to the apical cells in *Champia.*

In 1886, in a paper by N. Wille,† we again come across a study of *Lomentaria kaliformis.* He finds in this species a conical apical cell, which, dividing in several directions, sometimes parallel to its base, sometimes at right angles to the surface of the thallus, gives rise to other cells. These cells again divide into an inner small cell and an outer large one, the outer one dividing again into two. The outer cells are the only ones in which division continues. The inner ones do not divide, but, elongating, produce the longitudinal filaments. Wille hints that the diaphragms are derived from these filaments, but he does not tell how.

Summing this up, we see that Nägeli thinks there is a single apical cell in *Lomentaria kaliformis;* and Wille describes one very clearly for this species, but does not figure it. On the other hand, Berthold finds a cluster of apical cells in the tip of *Champia parvula*, of which he gives a diagram. The only thing bearing on the other problems suggested by our preliminary examination of *Champia* is Wille's hint that the diaphragms are derived from the filaments.

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* Berthold, Dr. G., Beiträge zur Morphologie und Physiologie der Meersalgen. Jahrbücher f. wiss. Botanik, Bd. XIII., 1882, p. 686.

† Wille, N., Beiträge zur Entwickelungsgeschichte der physiol. Gewebesysteme bei einigen Algengattungen. Bot. Centralblatt, 1886, VII., Qr. XXVI. p. 86.

My observations on the apical growth in *Champia* agree in the main with Berthold's, as far as his go. I do not find so great regularity here, however, as Berthold would give one to understand to exist. According to my observations, on looking down upon a tip of the plant, or in examining cross sections of it, a number of rows of cells are to be seen converging towards a common point, the apex (Figs. 4, 5, 6). Three or four of these rows meet at the apex, into the angles formed by them are pushed an equal number of other rows, and the remaining space is filled with a third series. I have found the number of these rows to vary from eleven to fifteen, but always to equal the number of longitudinal filaments in the branch, as Berthold has pointed out (Figs. 6 and 8). The reason for this will be seen when the origin of the latter is understood.

At the head of each of these rows, that is, at the part nearest its apex, there is a cell somewhat larger than those directly beneath it (Figs. 3 and 5). This cell gives rise to others of the row by anticlinal division; that is, by forming partitions at right angles at once to the surface of the frond and to the axis of the row. So each of these cells at the heads of the rows is a true apical cell (Scheitelzelle of the German botanists). Each one is in the shape of a triangular pyramid with rounded sides. The apex of the pyramid is directed inward, while the base lies at the surface of the frond. The length of the pyramid is 10 to 15μ, while the width at the base varies from 5 to 10μ. The cells formed by the division of the apical cells which are at the middle of the cluster, meet in the middle line below the apical cell (Fig. 3). And all of these daughter cells, whether they meet in the middle or not, appear somewhat crescent-shaped when close to their apical cell. They do not divide usually until removed several cells from it by division of the apical cell. They then divide, each by a partition parallel to the surface of the frond, at about a fourth or a third of the length of the cell from its inner end (Fig. 3). It is probable that the branches have their origin at this point, as explained later. The outer cell thus formed divides again into two or three cells (Fig. 6), and these may again divide. This division is by means of partitions which are at right angles to the surface of the plant and oblique to the original cell wall. The result of all this is the irregular mass of cells which forms the cortical layer or wall of the frond. The set of cells derived from each apical cell is easily distinguished within an area of forty micro-millimeters from the apex, because the cells having a common origin are separated from each other within this region by thinner cell walls than those separating cells of different origin, as shown in the figure. Below this area the cell walls become of equal thickness Cell division takes place chiefly within a short distance from the apex; below that, growth takes place principally by enlargement of the cells. Within the area of division the cells are filled with protoplasm and have very evident nuclei. The nuclei in the cortical layer are usually in the lower half of the cell. Below this area around the apex the cells contain large vacuoles and the nuclei become much less prominent, while the protoplasm becomes more coarsely granular. The inner cells above mentioned as the result of the first division below the apex do not divide at right angles to the surface of the plant; at least, if they do, it is a much less frequent process than in outer cells; but many of them, perhaps all, do divide once or twice by partitions parallel to the surface (Fig. 8). As the cortical layer grows, increasing the length and diameter of that part of the frond, these inner cells merely elongate, while they become separated laterally, and so form the longitudinal filaments; as described by Wille for *Lomentaria.*

By means of the division parallel to the surface just mentioned are produced the "bulb-cells," and the connections behind them with the cortical layers (Fig. 8). The "bulb-cells" attain their adult size very soon after their formation. At intervals of three cells or more, on certain filaments, division is carried further, until the processes pushed out from them in this way meet in the middle of the cavity (Fig. 9). The spaces between these processes are filled by similar ones from the other filaments, and in this way the diaphragm is formed. At first the diaphragm shows very plainly its origin in branches from the filaments. The cells are rounded, contain prominent nuclei, and in short look just like the young filament cells. Then the cells of each of the component branches are separated from each other by thinner walls than those which separate them from the other cells. This formation of the diaphragm occurs about thirty micro-millimeters from the surface of the apex. The young diaphragm keeps pace with the rapid growth of the adjacent parts of the plant, and thus preserves its continuity, by further cell division and by increase in the size of the cells. These cells finally become polygonal from mutual pressure, the cell walls become equally thick on all sides, and it becomes impossible to distinguish the cells, which had a common origin (Fig. 12). The original filament cell does not increase in diameter with the diaphragm cells, but becomes elongated with the other filament cells (Fig. 2).

It will be observed from the figures that the filaments that come from the apical cells nearest the middle of the cluster (Figs. 5 and 6) show more divisions than the others in the space above the young diaphragm (Fig. 8). The cells derived from them reach the centre of the diaphragm, while the others do not (Fig. 9), and these filaments are the first to give off bulb-cells below the diaphragm (Fig. 10). With the exception of the branches given off to form the diaphragm, the filaments do not branch. Each filament is perfectly simple and straight from its base to the apical cell at the other end.

The question as to the origin of the branches naturally arises now. I have not been able to get the earliest stages, but I am sure they are to be looked for very close to the apex of the plant, for the nearer you get to the apex the smaller branches you find. Occasionally, to be sure, branches a few chambers long may be found below much larger branches ; but still I think these are formed earlier than those above them, but are prevented from growth by some accident. It seems probable that the branch will be found to arise by division of one of the outer cells, already described as the result of the cell division close to the apex. At any rate, a branch was seen to spring from a point directly opposite a filament, in all the half-dozen cases that I examined concerning this.

Comparing my description of *Champia parvula* with the description of *Lomentaria kaliformis* by Nägeli and Wille, there will be noticed a striking similarity in general structure and in the details of growth, so far as either Nägeli or Wille describes them, except in regard to the apical cell. Further investigation is necessary to explain this remarkable difference in two species otherwise so much alike.

In order to see if they might throw any light on my subject I have made a hasty examination of some alcoholic material of *Champia salicornoides*, Harv., from Key West, and of *Lomentaria Baileyana.* The former has an apical growth identical with that in *Champia parvula*, and does not differ very greatly in structure from that species. The frond is much larger, but the individual cells are of about the same size. The branches in *Champia salicornoides* do not come off at the nodes, but may spring from any part of the internodes. At the base of each branch is a layer of cells smaller than those in the wall of the main stem, but it is apparently a continuation of that structure. Then inside of this is a circular patch of rounded cells twice as large as the ordinary cells of the wall. So that the basal chamber of the side branch is separated from the chamber of the main branch by two layers of cells. There are a good many more filaments in this species than there are in *Champia parvula*, and each filament has about seven cells to a chamber. On each of the filament cells except those piercing the diaphragms there is a bulb-cell, or there may be a pair of them together. The cells that connect the filaments with the cortical layer are sometimes enlarged, and bear bulb-cells similar to those on the filaments. The branches spring from a cortical layer directly opposite a filament, as in *Champia parvula*, and in the one specimen that I examined on this point I found a bulb-cell at the centre of the base of the branch.

Lomentaria Baileyana is very different from *Champia*. There are no diaphragms in the frond except across the base of the branches. Inside the cortical layer, which resembles the one in *Champia*, is a network with rather small meshes, composed of oblong cells whose long axes run more or less obliquely in the direction of their part of the plant. Inside of this network is another, with large meshes, and formed by slender crooked and branched filaments, on which are found occasionally bulb-cells like those in *Champia*. The filaments seem to come together at the tip in a sort of tuft, in which I can see no regular order.

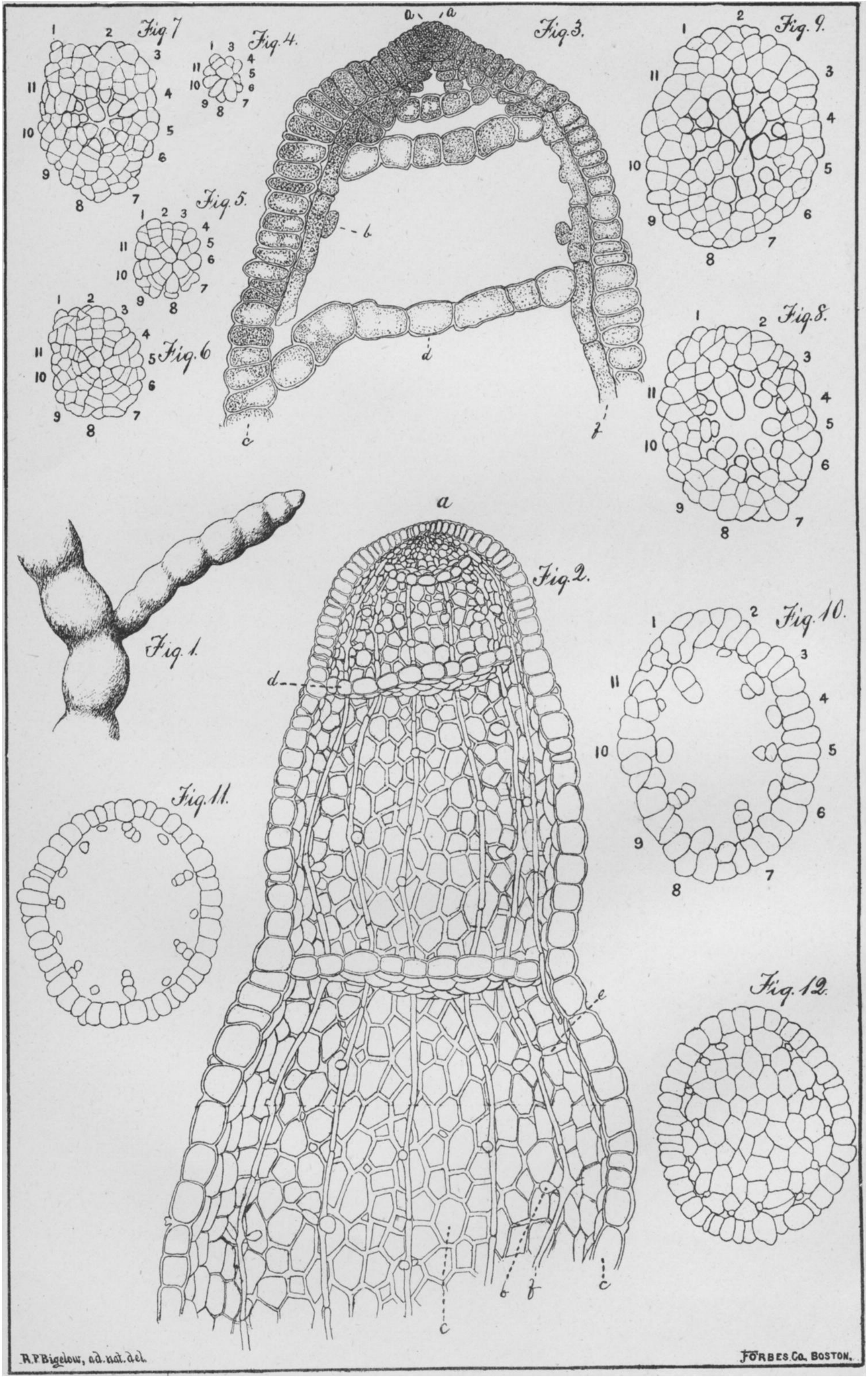
I have also examined some dried material of *Lomentaria Coulteri*. The main stems of this plant are without constrictions and solid, while the small side branches are chambered, and superficially resemble *Champia*. The whole plant is covered with a cortical layer of small columnar cells, well filled with protoplasm, and containing the coloring matter. The bulk of the main stem is of ordinary parenchyma, the cells containing but little protoplasm. The chambered branches have a single layer of this tissue lining the cortex, and it also forms the single-layered diaphragms. The filaments in the chambered portion somewhat resemble those in *Lomentaria Baileyana*, but resemble more closely those in *Champia parvula*. They plainly converge to a point at the apex of the branch; but just what the structure is there, the material was insufficient to show.

We have to leave our subject for the present in an unsettled, and therefore rather unsatisfactory condition. In order to get a complete understanding of these hollow-fronded sea-weeds, the development of one or more of them must be traced from the spore to the adult stage. The present paper can, however, lay claim to having added its little to our knowledge of these plants, in making clear, — 1. That in the case of *Champia parvula* the apical growth is not from a single apical cell, but, as Berthold has pointed out, from a cluster of them; 2. That each of these apical cells is morphologically at the tip of one of the longitudinal filaments; 3. That in the three or four cells which seem to be morphologically the tip of the filament each cell divides, part going to form parts of the adult filament, the rest to join in the formation of the cortex; 4. That the diaphragms and bulb-cells are alike in origin, in being formed by outgrowths from the filaments; and, 5. It would appear from the limited number of observations made on this point that the branches always have their origin opposite a filament.

NOTE.

In October, 1886, Mr. Bigelow, then a candidate for the degree of Bachelor of Science, undertook, at my suggestion, the investigation the results of which are given in the preceding pages. At the time, I was not aware that any other botanist was working on the same subject, and it was not until April, 1887, that I learned from the "Botanisches Centralblatt" that Professor F. Debray had just published a paper entitled "Recherches sur la Structure et le Développement du Thalle des *Chyclocladia*, *Champia* et *Lomentaria*," covering the same ground as that on which Mr. Bigelow was at work. I was unable to obtain a copy of the original paper of Professor Debray, published in the "Bulletin Scientifique du Département du Nord," IX. 253–266, until late in May, and as at that time Mr. Bigelow had practically finished his work, it seemed to me best that he should publish his results, although they were in accord with those of Professor Debray. It should be said, in explanation of the omission by Mr. Bigelow of any reference to Professor Debray's paper, that he did not see a copy of it until after his own paper was quite finished and in my hands for publication. Had I known at an earlier day that Professor Debray was at work on this subject, I should, of course, have suggested a different topic to Mr. Bigelow. As it is, his work is a confirmation of previous results reached quite independently, because, as I have said, he was in complete ignorance of what had been written by Professor Debray until after his article was finished.

W. G. Farlow.



R.P. Bigelow, ad. nat. del.

FORBES Co. BOSTON.

EXPLANATION OF THE PLATE.

All the figures are of *Champia parvula*. Fig. 2 is from a free-hand section mounted in glycerine and acetic acid. It is drawn chiefly with the camera-lucida, but in places is slightly diagrammatic. The other figures are strictly camera-lucida drawings. Those beyond Fig. 2 are made from stained microtome sections mounted in benzol balsam.

Fig. 1. A small branch, with a portion of the larger one from which it sprang. $\times \frac{20}{1}$.

Fig. 2. Interior view of the upper portion of a branch. *a*, apex; *b*, bulb-cell; *c*, cortex; *d*, diaphragm; *f*. filament; *e*, connection between the filament and the cortex. $\times \frac{140}{1}$.

Fig. 3. Longitudinal section of a tip passing through the apex. *a*, apical cell; the other letters as above. $\times \frac{280}{1}$.

Figs. 4–10. A series of transverse sections from a single tip. They are about 5μ thick. Figs. 4-7 are a continuous series, Fig. 4 being the extreme tip. Figs. 8 and 9 are the sixth and seventh sections of the series, and Fig. 10 is the tenth. Figs. 4, 5, and 6 show the converging rows of cells, each headed by an apical cell. In Fig. 7 we get the beginning of the cavity. Fig. 8 shows the condition just above the young diaphragm, which appears in Fig. 9. Fig. 10 is the first section that cleared the diaphragm below. By comparing with Fig. 3, it will be seen that these sections are oblique to the axis of all the cells in them, except those very near to the middle of the section. 1, 2, 3, etc., indicate corresponding areas in the different sections. $\times \frac{280}{1}$.

Fig. 12. Transverse section of another branch through the third diaphragm.

Fig. 11. Second section above Fig. 12. In these two sections we have very nearly the adult condition. $\times \frac{140}{1}$.